LETTER

Selection against immigrants in wild seabird populations

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Abstract

Immigration is a major demographic parameter shaping population dynamics and is an important driver of eco-evolutionary patterns, but the fitness consequences for individuals following their settlement to a new population (immigrants) remain poorly tested in wild animal populations, particularly among long-lived species. Here we show that immigrants have a lower fitness than residents in three wild seabird populations (wandering albatross *Diomedea exulans*, southern fulmar *Fulmarus glacialoides*, snow petrel *Pagodroma nivea*). Across all species and during a 32-year period, immigrants made on average −9 to 29% fewer breeding attempts, had 5–31% fewer fledglings, had 2–16% lower breeding success and produced 6–46% fewer recruits. Female immigration and male residency were also favored through differences in breeding performance. We provide evidence for selection against immigrants in wild populations of long-lived species and our results are consistent with female-biased dispersal in birds being driven by asymmetric limiting resources and the competitive ability of dispersers vs. non-dispersers.

Keywords

Dispersal, fitness, immigrant, seabirds, sex-biased dispersal.

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INTRODUCTION

Dispersal is a crucial driver of ecological and evolutionary patterns because of its direct implication on processes such as gene flow, effective population size, genetic drift, local adaptation, inbreeding, colonisation and viability of populations and species (Clobert *et al.*, 2001). Among the various aspects of dispersal, theoretical and empirical studies suggest that immigrant fitness following settlement to a new population may play an important role in population genetic processes such as local adaptation and speciation (Slatkin, 1985; Hendry, 2004; Nosil *et al.*, 2005; Clobert *et al.*, 2012), and in population persistence and resilience (Ward, 2005; Lowe and Allendorf, 2010; Schaub *et al.*, 2013). Although many empirical studies have compared immigrants (successful between-population dispersers) and residents (individuals remaining in their natal population) performance in wild animals, settlement costs of dispersal are poorly documented and the overwhelming majority of these studies focused on a single demographic trait (generally survival or number of offspring) used as a fitness proxy (Bonte *et al.*, 2012). However, immigrant and resident performance may be trait-specific (Bensch *et al.*, 1998) and since fitness integrates several demographic components, single trait approaches may be misleading. Furthermore, the few studies that compared immigrant and resident fitness using multiple traits approaches are strongly biased towards short-lived species (Verhulst and Van Eck, 1996; Bensch *et al.*, 1998; Hansson *et al.*, 2004; Martinig *et al.*, 2020; but see Oro *et al.*, 2011). This is due to a lack of empirical data which are difficult to collect in wild animal populations as it requires both identifying true immigrants in study populations and the following of their survival and fecundity over multiple years. This is extremely challenging in long-lived species, and more particularly in species with great potential for long-range dispersal such as seabirds (Inchausti and Weimerskirch, 2002). In addition, contrary to species with

short generation time, long-lived species generally spend several years exploring their environment before recruiting (Weimerskirch, 2001). During these years they may get familiarised with new environments and acquire the same skills as residents. Therefore, there is a major research gap regarding our understanding of the performance of immigrants and residents in long-lived species based on multiple trait approaches.

Sexes also often differ in the propensity and/or distance of dispersal (Trochet *et al.*, 2016). Females disperse more frequently and further away than males in birds, the opposite pattern being typical in mammals, while unclear patterns are observed in other species. Theoretical studies have proposed several hypotheses to explain sex-biased dispersal (Greenwood, 1980; Perrin and Mazalov, 1999; Li and Kokko, 2019), the prevailing ones being asymmetric limiting resources, within- and across-generation kin competition, inbreeding avoidance, fitness variance and effects of genetic architecture, but extremely few have explicitly integrated the reproductive value of an immigrant male or female relative to that of a philopatric individual of the same sex (Perrin and Mazalov, 1999). In all cases, empirical information on the relative fitness of immigrants and residents in relation to sex is generally lacking (Martinig *et al.*, 2020) and is needed to test predictions from theoretical models.

Here, we use long-term demographic data over a 32-year period for three long-lived seabird species (the wandering albatross *Diomedea exulans*, southern fulmar *Fulmarus glacialoides* and snow petrel *Pagodroma nivea*) to investigate whether immigrants and residents differ in four metrics of fitness after recruitment. We first use capture-mark-recapture data to estimate four key demographic rates - probabilities of survival, breeding (i.e. laying an egg), hatching an egg and fledging a chick - of immigrants and residents by considering different breeding states and accounting for imperfect recapture probability. Second, we test whether demographic rates differ between immigrants and residents for each species and

each sex. Third, we estimate and compare four metrics of individual fitness for immigrants and residents: number of breeding events, defined as the total number of occasions spent by an individual in the breeding state; number of off-spring fledged, defined as the total number of offspring fledged by an individual; breeding success, defined as the ratio between number of offspring fledged and number of breeding events; and number of recruits, defined for each individual as the total number of offspring fledged that recruited in the study population.

MATERIALS AND METHODS

Study areas

Wandering albatrosses were monitored at Ile de la Possession (46°24'S, 51°46'E), Crozet archipelago, south western Indian Ocean. Wandering albatrosses nest in loose aggregations forming eight breeding colonies that are located in flat boggy areas on the northern and eastern coasts of the island. The population had *c*. 500 breeding pairs in the 1960s, declined steeply in the 1970s to reach 260 pairs and increased progressively to 390 pairs in 2017 (Weimerskirch *et al.*, 2018).

Southern fulmars were monitored on Ile des Pétrels (66°40'S, 140°01'E), Pointe Géologie archipelago, Terre Adélie, Antarctica. Fulmars nest in a dense aggregation at a single colony on a rocky cliff on the island. The population has increased from 30 breeding pairs in the early 1960s to 55 in 2017 (Jenouvrier *et al.*, 2003).

Snow petrels were monitored on the Pointe Géologie archipelago, Terre Adélie, Antarctica. Snow petrels nest in cracks or under boulders situated in rocky areas on eight islands (which vary in size from 2 to 20 ha) of the archipelago, either in dense colonies or in loose aggregations. The population is relatively stable with 440 breeding pairs on the Ile des Pétrels and 213 pairs breeding on the other islands of the Pointe Géologie archipelago in 2017 (Micol and Jouventin, 2001).

For all species the nearest neighbouring breeding populations outside the Ile de la Possession and the Pointe Géologie archipelago are shown on Figure 1.

Data collection and identification of immigrants

Long-term capture-mark-recapture monitoring of wandering albatross started in 1965 and of southern fulmar and snow petrel in 1963 (Supporting Information S1). To be considered
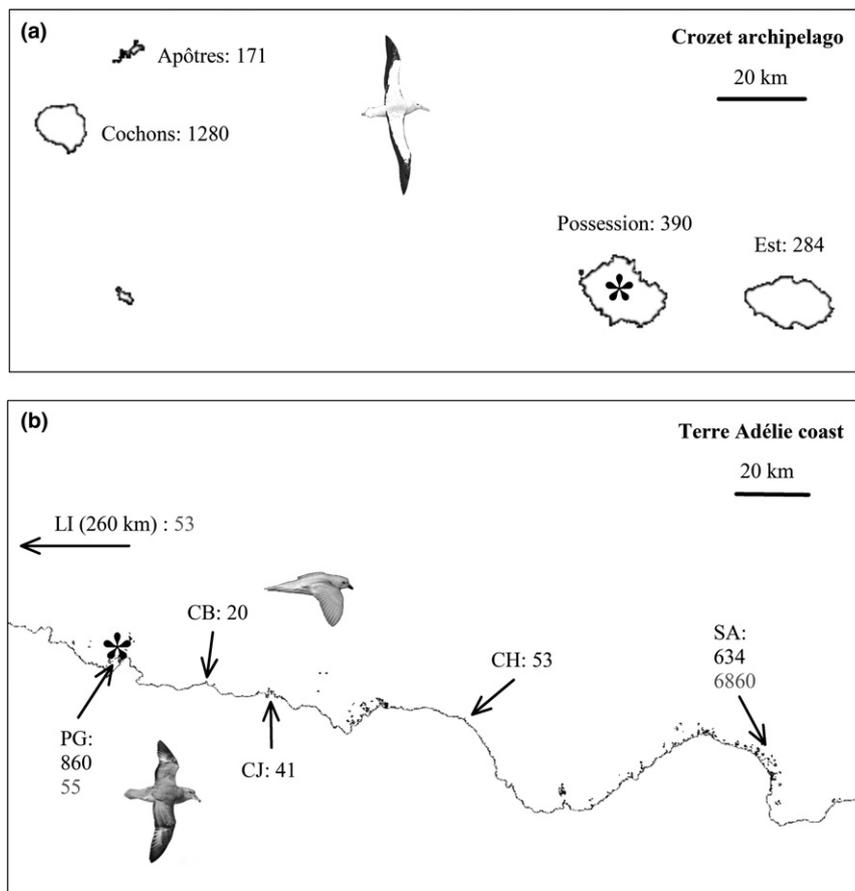

Figure 1 Map showing the two main study areas (a) Ile de la Possession within the Crozet archipelago for wandering albatrosses, and (b) Pointe Géologie archipelago on the Terre Adélie coast for southern fulmars and snow petrels. Numbers are breeding pairs from Weimerskirch *et al.* (2018) [wandering albatross]; Law (1962) for LI, Barbraud *et al.* (1999) for SA, 2017 for PG [southern fulmar]; Barbraud *et al.* (1999) for CP, CJ, CH, SA, and 2017 for PG [snow petrel]. PG: Pointe Géologie; CB: Cap Bienvenue; CJ: Cap Jules; CH: Cap Hunter; SA: Stillwell archipelago; LI: Lewis Island. Numbers in grey indicate southern fulmars. Stars indicate location of study colonies.

as a resident, an individual had to be born in the population (i.e. Ile de la Possession for wandering albatrosses, Ile des Pétrels for southern fulmars and Pointe Géologie archipelago for snow petrels) and recorded as having successfully recruited (i.e. acquired a nest site and breeding) or successfully returned (i.e. acquired a nest site and not breeding) to their natal population in at least one census during the years following their birth. To be considered an immigrant, an individual had to be unringed at first capture and recorded as having successfully recruited (i.e. acquired a nest site and breeding) or successfully returned (i.e. acquired a nest site and not breeding) to the studied populations defined above (i.e. Ile de la Possession, Ile des Pétrels and study colonies for wandering albatrosses, southern fulmars and snow petrels respectively) (Supporting Information S2).

The accuracy with which we distinguish immigrants relies on how successfully all nests were found and all chicks were ringed in the study populations. We are confident that over the study periods during which systematic chick ringing occurred (1965–2017, 1963–2017 and 1990–2017 for wandering albatrosses, southern fulmars and snow petrels respectively) chicks in at least 99% of successful nests of wandering albatrosses, 100% of successful nests of southern fulmars and 95% of successful nests of snow petrels were ringed. Reasons for this high efficiency at ringing fledglings are: (1) fieldworkers visited the colonies of the three species each year since the initiation of the long-term studies thanks to the unconditional support of the French Polar Institute; (2) all species are conspicuous and nests are unlikely to be missed by observers; (3) multiple visits were made to breeding colonies during each breeding season; (4) small area and size of the southern fulmar colony; (5) well defined area of wandering albatross colonies; (6) all detected nest sites of snow petrel in the Pointe Géologie archipelago have been marked with paint since the beginning of the monitoring of the entire archipelago in 1990. Since immigrants were unringed at their first capture, their age was not known. Therefore, we assumed immigrants were the same age as residents at return or recruitment.

Modelling vital rates

We considered observations of residents and immigrants monitored during the period 1985–2017 for wandering albatrosses and southern fulmars, and during the period 2004–2017 for snow petrels to build encounter histories. For every individual, its encounter history started at the first return to breed at a study population. The sex of each individual was known for wandering albatrosses and snow petrels. We analysed the capture histories of 1748 female wandering albatrosses (335 immigrants and 1413 residents), 1665 male wandering albatrosses (234 immigrants, 1431 residents), 395 southern fulmars (160 immigrants and 235 residents), 158 female snow petrels (95 immigrants and 63 residents) and 127 male snow petrels (79 immigrants and 48 residents). To estimate demographic parameters and fitness while taking into account imperfect detectability of marked individuals, we used multi-state capture-mark-recapture (MSCMR) models (Brownie et al., 1993; Lebreton et al., 2009).

For southern fulmars and snow petrels, we estimated the following demographic parameters: survival probability (Φ) as the probability that an individual survives from year t to $t + 1$, breeding probability (β) as the probability that an individual breeds (i.e. lay an egg) in year $t + 1$ given that it survived, hatching probability (δ) as the probability that an individual hatches its egg in year $t + 1$ given that it bred and survived, fledging probability (γ) as the probability that an individual fledges a chick in year $t + 1$ given that it hatched its egg, bred and survived, and recapture probability (p). To do so, we constructed a MSCMR model (Supporting Information S3 and Fig. S1) with five states consisting of one non-breeder state (NB), three breeder states [failed breeder at the egg stage (FBE), failed breeder at the chick stage (FBC), successful breeder (SB)] and the dead state (†). Capture histories were coded considering five events corresponding to field observations: 0 = not observed, 1 = seen as NB, 2 = seen as FBE, 3 = seen as FBC, 4 = seen as SB. The dead state was not observable.

Since wandering albatrosses have a quasi-biennial breeding strategy (Barbraud and Weimerskirch, 2012), we estimated an additional parameter for this species: the return probability (ρ) as the probability that an individual returns to its nest in year $t + 1$ given that it survived. To do so, we constructed a MSCMR model (Supporting Information S3 and Fig. S2) with eight states consisting of one non-breeder state (NB), three breeder states [failed breeder at the egg stage (FBE), failed breeder at the chick stage (FBC), successful breeder (SB)], three non-observable states [post-non-breeder state (PNB), post-failed breeder state (PFB), post-successful breeder state (PSB)] and the dead state (†). Capture histories were coded as for the two other species. The dead state was not observable.

First, we developed null models for each species where all parameters were state dependent but were equal between immigrants and residents, and where all mathematical parameters were identifiable. To allow parameter identifiability, for southern fulmars and snow petrels, the underlying parameters Φ, β, δ and γ describing the transition probabilities to and from aggregated breeding states FBE, FBC and SB (but not NB) were the same. Thus, only the underlying parameters for the non-breeding and breeding states were distinguished. For wandering albatrosses, the underlying parameters Φ from aggregated breeding states FBE, FBC, SB, PNB, PFB and PSB were the same (the state NB was kept separate), and the underlying parameters ρ, β, δ and γ were the same to and from the following state aggregations (FBE, FBC, SB), (PNB, PFB, PSB) and NB. Thus, only the non-breeding and breeding states were distinguished for parameter Φ, and non-breeding, breeding and post-breeding states were distinguished for the other demographic parameters. Recapture probabilities were entirely state and time dependent. All the mathematical parameters were estimated for these models, which were considered as appropriate for further modelling.

Second, the goodness of fit tests (GOF) for multistate models (Pradel et al., 2003) were performed on the null models using the software U-Care (Choquet et al., 2009a) to test whether these models fitted the data. We ran the test on the JollyMoVe (Brownie et al., 1993) umbrella model for multistate data (see Supporting Information Table S1).

Third, we performed model selection using program E-SURGE (Choquet *et al.*, 2009b) to test for the effects of group (immigrant vs resident) on demographic rates and recapture probability. Model selection was done using the Akaike Information Criterion (AICc) (Burnham and Anderson, 2002). First, we considered that model i received better support compared to the null model when the ΔAICc was < -2, where ΔAICc = AICc$_i$ – AICc$_{null\ model}$ (Burnham and Anderson, 2002). Second, and following (Anderson and Burnham, 2002) and (Arnold, 2010), we report all models and discuss support of alternative models depending on the level of reduction in deviance *vs.* the null model. If an alternative model was within 2 AICc units from the null model and with a very similar value of the deviance we considered model i as not supported (Burnham and Anderson, 2002). Thus, we considered immigrants and residents did not differ. We first modelled the recapture probability and then the demographic parameters one by one.

Estimating fitness

We estimated four parameters as different metrics for individual fitness. First, we used the total number of offspring fledged by an individual (NOF) during the study period. We used the counting algorithm to estimate NOF (Rouan *et al.*, 2009). This method takes into account the uncertainty about the reproductive status when the individuals are not detected or when the reproductive status cannot be assessed. The method uses the parameters of the MSCMR model estimated using program E-SURGE and applies them to each encounter history so as to provide for each encounter history the probability that an underlying state *s* has occurred *n* times between the first capture and the last capture occasion. From these, the average number of occasions in state *s* can be calculated. NOF is then estimated as the sum of the number of occasions in the state successful breeder during the study period.

Second, we used the number of breeding events (NBE), defined as the number of years spent by an individual in the breeding state. NBE was estimated using the same method as NOF, and was the sum of the number of years in any of the breeder states during the study period.

Third, we used average breeding success (BS), defined as the average number of offspring fledged per breeding attempt. BS was calculated as the ratio NOF/NBE.

We calculated NOF, NBE and BS for immigrants and residents using models where recapture probabilities were the same for immigrants and residents and all other demographic parameters differed (see model selection results). To take uncertainty of demographic parameter estimates into account and to test for differences in NOF, NBE and BS between immigrants and residents we used the parametric bootstrap for the counting algorithm with 100 bootstrap samples. We then used Student's *t*-tests or Mann–Whitney rank sum tests to test for differences in NOF, NBE and BS between immigrants and residents. Estimates are reported as means $\pm$ 1 SE. Significance was set at $\alpha = 0.05$. All NOF and NBE estimates were performed using program E-SURGE.

Fourth, we used the number of recruits (NRC), defined for each individual as the total number of offspring fledged that recruited in the study population during the study period.

Recruits are offspring recaptured as breeding at the study sites. Since recapture probability was high (>0.90) for breeding individuals of the three studied species, we are confident that the observed number of local recruits was close to the true number of recruits. The distribution of the number of recruits showed a high number of zero values (i.e. a high number of individuals produced no recruits). We thus fitted zero-inflated negative binomial or Poisson distribution generalised mixed effect models with 'year' as a random effect using the 'glmmTMB' package in R (Brooks *et al.*, 2017) to test for statistically significant differences in NRC between residents and immigrants while controlling for random annual variation. We used the function 'fitdist' from the package DHARMa to assess the fit of residuals (see Fig. S1; Fig. S2; Fig. S3). NRC was only estimated for southern fulmars and wandering albatrosses. Indeed, snow petrel data set covered the period 2004–2017 (see above), and since mean age at first breeding is 9.9 (min: 5, max: 14) years (Chastel *et al.*, 1993), there were too few recruits to perform this analysis.

RESULTS

We recorded 3134 residents and 874 immigrants for all species and sexes combined. The mean ($\pm$ 1 SE) annual immigration rate, estimated as the proportion of recruits that were immigrants as opposed to residents in the studied areas, was 0.157 ± 0.054, 0.623 ± 0.036 and 0.348 ± 0.038 for wandering albatrosses, snow petrels and southern fulmars respectively. Despite annual fluctuations there was no temporal trend in immigration rates (linear models: southern fulmar, $P = 0.085$; wandering albatross, $P = 0.361$; snow petrel, $P = 0.223$).

Modelling vital rates

Model selection provided strong evidence that recapture probabilities did not differ between immigrants and residents for the three species (Supporting Information Table S2). There was also strong evidence that several demographic parameters differed between immigrants and residents, including fledging probability in male snow petrels (model M17), hatching probability in female snow petrels (M24), and breeding probability in southern fulmars (M31) (Table S2). For several other parameters, although ΔAICc were < 2, there was reduction in deviance for alternative models compared to the null models, supporting differences between immigrants and residents (Table S2). For male wandering albatrosses reduction in deviance for models M4 and M7 compared to M1, suggested that immigrant males had lower hatching (0.716 ± 0.052) and survival (0.946 ± 0.009) probabilities than residents (0.794 ± 0.015 and 0.962 ± 0.003 respectively), particularly for individuals that were breeders the previous year (Fig. 2). For female wandering albatrosses, there was support for lower hatching, breeding probability and survival probabilities (but higher return probability) for immigrants (Table S2 models M11, M12, M13, M14; Fig. 2). For male snow petrels, there was support for lower survival probability for immigrants, but higher breeding probability (Table S2 models M17, M18, M20; Fig. 3a). For female snow petrels, there was support for
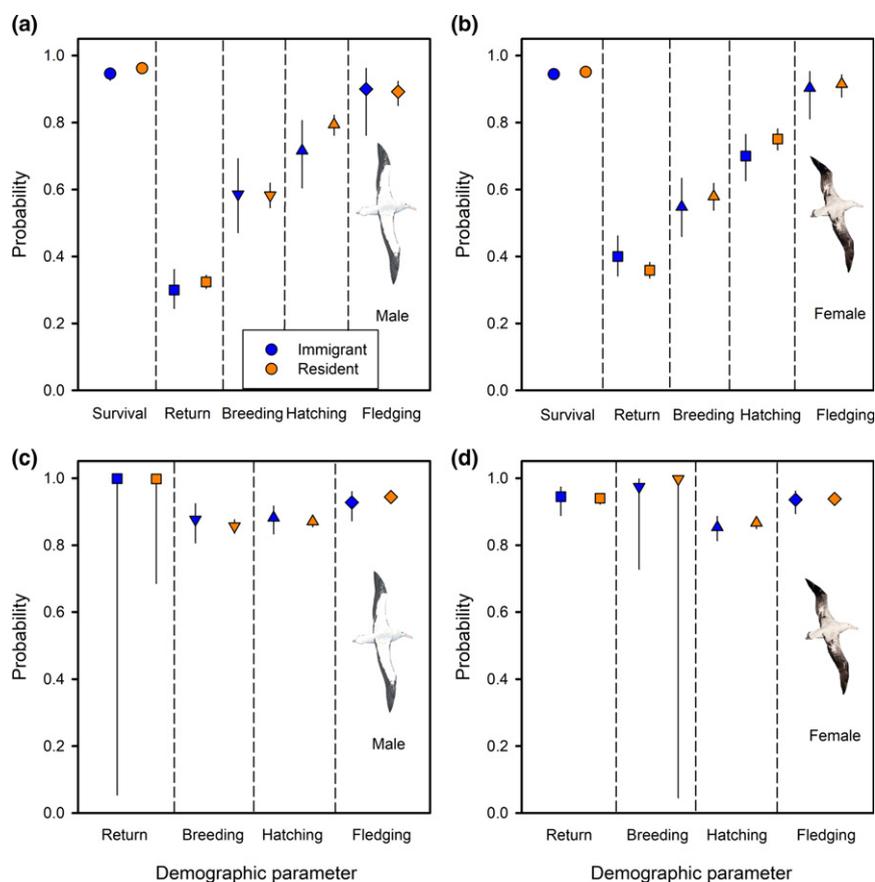
Figure 2 Demographic parameters of immigrant and resident wandering albatrosses. (a) Males that were breeding the previous year. (b) Females that were breeding the previous year. (c) Male that were in sabbatical the previous year. (d) Females that were in sabbatical the previous year. Error bars indicate 95% confidence intervals. The survival probabilities were constrained to be similar for individuals that were breeding the previous year and for those that took a sabbatical year.

lower breeding probability for immigrants (Table S2, models M24, M25; Fig. 3b). For southern fulmars, there was support for lower fledging and hatching probabilities for immigrants (Table S2, models M29, M30, M31; Fig. 3c). Overall, differences in deviance, ΔAICc values and parameter estimates provided moderate to strong evidence for higher demographic performance of residents, and for a few demographic parameters immigrants outperformed residents (breeding probability in male snow petrels and hatching probability in female snow petrels).

Estimating fitness

Across all species, immigrants made on average 4–29% fewer breeding attempts and had 6–31% fewer fledglings relative to immigrants (Fig. 4a and b). Only immigrant southern fulmars made 9% more breeding attempts than residents, and immigrant female snow petrels had 7% more fledglings than residents (Fig. 4a and b). Breeding success across all species showed that immigrants had 2–16% lower success than residents (Fig. 4c).

The sex ratio for immigrants was female biased (58.9% females, $n = 569$, binomial test $P < 0.001$) in wandering albatrosses (but not for residents: 49.7%, $n = 2844$, binomial test

$P = 0.750$) and the sex ratio for immigrant and resident snow petrels was not significantly biased (immigrants: 54.6%, $n = 174$, binomial test $P = 0.255$; residents: 56.8%, $n = 111$, binomial test $P = 0.184$), but sample sizes were relatively small. Immigrant males made on average 8–37% fewer breeding attempts and produced 17–38% fewer fledglings relative to resident males (Fig. 4a and b). The same differences were observed between immigrant and resident females (1–21% fewer breeding attempts and −7 to 23% fewer fledglings; Fig. 4a and b), although these differences were lower than in males by a factor of 1.8–13.7 and 1.6–3.4 respectively. Immigrant males had 2–10% lower breeding success than residents, immigrant female wandering albatrosses had 3% lower breeding success than residents, but immigrant female snow petrels had 7% higher breeding success than residents (Fig. 4c).

On average, immigrant individuals produced 6–46% fewer recruits than residents (male wandering albatrosses: 45.9%; female wandering albatrosses 16.5%; southern fulmars 6.4%; Fig. 5). However, differences were only statistically significant for wandering albatrosses (Table 1). A higher proportion of immigrant albatrosses failed to produce recruits compared to residents (females: $P = 0.044$; males: $P < 0.001$). Among individuals that produced at least one recruit, residents tended to produce more recruits than immigrants (Fig. 5) but the
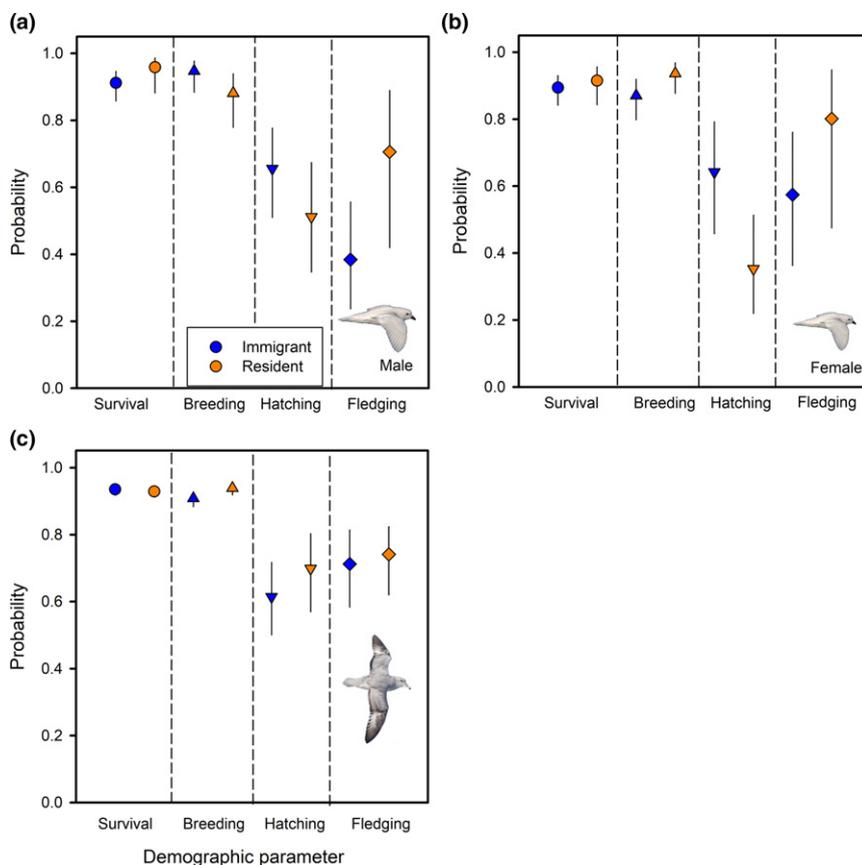
Figure 3 Demographic parameters of immigrant and resident snow petrels and southern fulmars. (a) Male snow petrel. (b) Female snow petrel. (c) Southern fulmar. Error bars indicate 95% confidence intervals.

differences were not statistically significant for all species and sexes (Table 1).

DISCUSSION

Direct comparison of four fitness metrics of immigrants and residents among three seabirds enabled us to assess fitness costs after dispersal in long-lived species. Immigrants had generally lower fitness than residents. This is in line with the results from a previous study on fish (Peterson *et al.*, 2014) and some studies of birds (Verhulst and Van Eck, 1996; Bensch *et al.*, 1998) and mammals (Martinig *et al.*, 2020), but is not consistent with others (birds: Gienapp and Merilä, 2011; Germain *et al.*, 2017; mammals: Waser *et al.*, 2013). In another long-lived species, the Audouin's gull *Larus audouinii*, Oro *et al.* (2011) compared fitness components among residents and immigrants and found differences in recapture probabilities, suggesting higher site-tenacity for residents than for immigrants, but similar survival and recruitment. However, they did not use integrative metrics such as ours to estimate fitness. Since high dispersal ability is related to several aspects of fast life-history strategies (Stevens *et al.*, 2012, 2014; Beckman *et al.*, 2018) one may expect lower costs of dispersal in short-lived species (whose life-history traits should be shaped for dispersal) than in long-lived species. Also, the predicted and observed negative co-variation between spatial

and temporal dispersal across species (Buoro and Carlson, 2014) may suggest lower costs of spatial dispersal for short-lived species, as long-lived species typically achieve temporal dispersal though age structure and iteroparity. However, strong association between high dispersal and high fecundity, but also positive association with survival rate, points towards complex dispersal-related life-history syndromes, whose demographic consequences remain very poorly known and require further research (Buoro and Carlson, 2014; Stevens *et al.*, 2014).

Differences in demographic parameters between immigrants and residents suggest that this selection against immigrants resulted from both immigrant inviability (Nosil *et al.*, 2005) and immigrant infecundity (Smith and Benkman, 2007) (most frequently, immigrants were less successful at fledging chicks and, to a lesser extent, bred less frequently and hatched fewer eggs). It should be noted that these are apparent survival estimates, thus confounding true mortality and permanent emigration. Therefore, the lower apparent survival of immigrants relative to residents may be due to higher mortality and/or higher emigration from the study sites. Nevertheless, dispersal of breeding wandering albatrosses outside the study area is extremely low (Inchausti and Weimerskirch, 2002). Likewise, the lower number of recruits produced by immigrants might partly result from differential emigration rather than survival if immigrants have offspring that are more likely to recruit
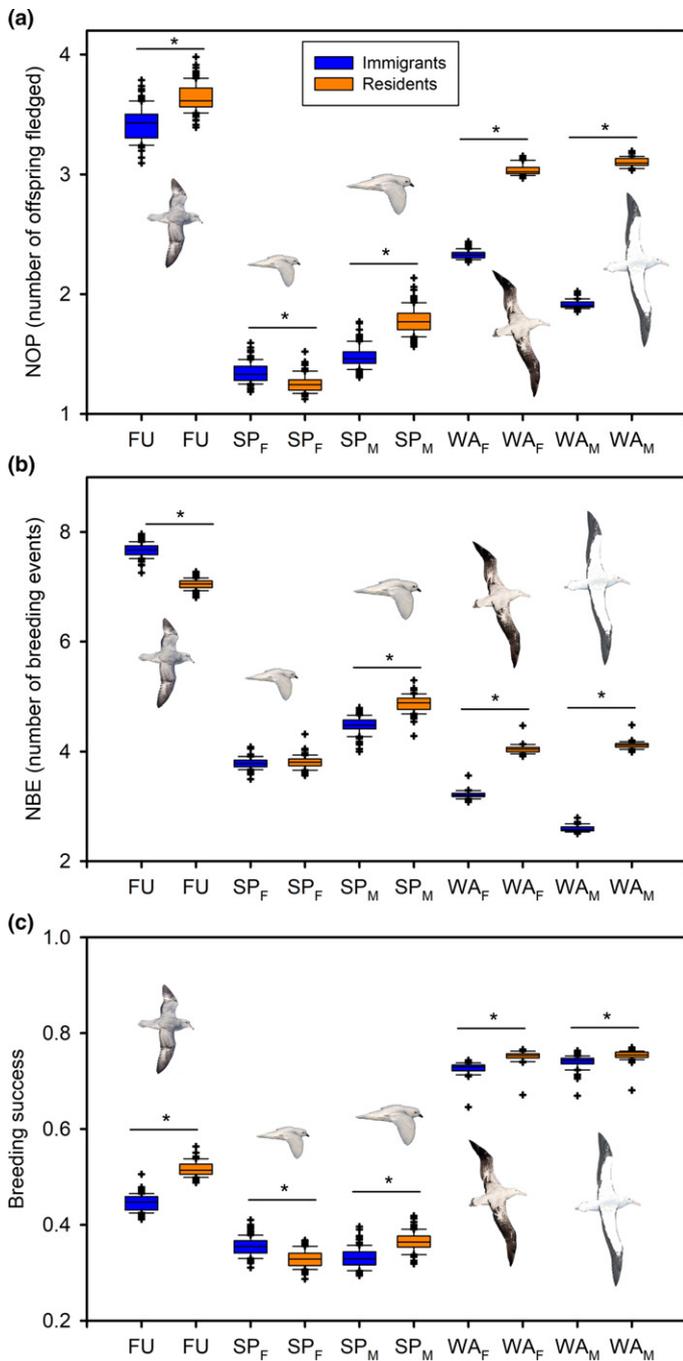
Figure 4 Fitness metrics of immigrant and resident individuals in three seabird species. (a) Number of offspring fledged. (b) Number of breeding events. Center line, median; box limits, lower and upper quartiles; error bars, 90th and 10th percentiles; crosses, outliers. * indicates significant differences. FU = southern fulmar, SP = snow petrel, WA = wandering albatross. Subscripts F and M respectively indicate female and male.

Figure 5 Number of recruits produced by immigrants and residents in two seabird species. (a) male wandering albatrosses. (b) female wandering albatrosses. (c) southern fulmars. * indicates significant differences. R indicates that only resident southern fulmars produced more than four recruits.

elsewhere. This has been found in a handful of species (Hansson *et al.*, 2003), including the wandering albatross although only on short spatial scales between neighbouring colonies (Charmantier *et al.*, 2011). Due to lower fitness of immigrants, we conclude that gene flow was lower than immigration rate. However, this is unlikely to promote genetic differentiation between populations of the studied species since the
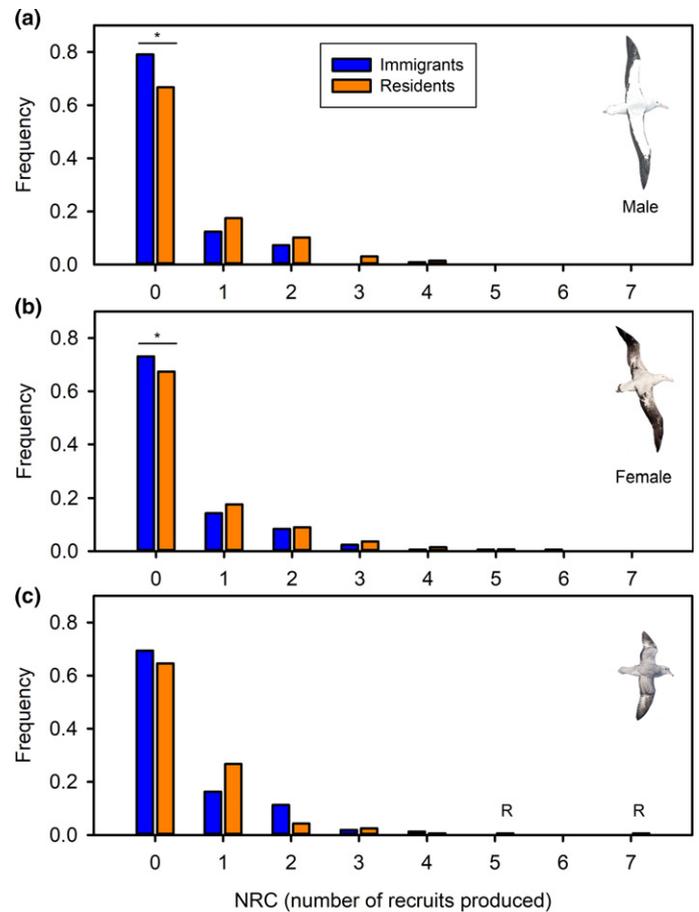
proportion of immigrant recruits was high compared to the level of gene flow necessary to maintain panmictic populations (one effective immigrant per generation). Indeed, populations of wandering albatrosses exhibit little genetic differentiation across the species' range (Milot *et al.*, 2008) as do populations of snow petrels in East Antarctica (Carrea *et al.*, 2019). Nevertheless, our results imply a lower contribution of immigrant recruits in population dynamics as compared with resident recruits.

Minimum dispersal distances for immigrants belonging to the three studied species ranged from 23 to 175 km, depending on the species considered. Our analyses thus suggest that individuals potentially immigrating from relatively short distances (for seabirds) can experience lower fitness following settlement (Hansson *et al.*, 2004). For wandering albatrosses, which have been marked at other breeding localities, we recorded in our study population one immigrant from Ile de l'Est (23 km, Crozet archipelago), four from Marion Island (1070 km), seven from Kerguelen Islands (1320 km) and one from South Georgia (6030 km). However, these numbers are unlikely to reflect site-specific immigration rates since there are massive differences in ringing effort between the various

Table 1 Parameter estimates from the generalised linear mixed effect models outputs with number of recruits as a response variable for residents and immigrants of wandering albatrosses (males and females) and southern fulmars

Fixed and random effects*	Group	Estimate	SE	Z	P
Male wandering albatross, *n* = 1665					
Conditional model	Intercept	−0.053	0.205	−0.260	0.795
	Resident	0.128	0.209	0.613	0.540
Zero-inflation model	Intercept	1.328	0.161	8.269	<0.001
	Resident	−0.632	0.170	−3.715	<0.001
Year		0.147	0.383		
Female wandering albatross, *n* = 1748					
Conditional model	Intercept	0.277	0.140	1.974	0.048
	Resident	−0.215	0.139	−1.552	0.121
Zero-inflation model	Intercept	1.001	0.123	8.125	<0.001
	Resident	−0.273	0.136	−2.012	0.044
Year		0.156	0.395		
Southern fulmar, *n* = 321					
Conditional model	Intercept	0.028	0.226	0.125	0.900
	Resident	−0.316	0.305	−1.036	0.300
Zero-inflation model	Intercept	0.818	0.172	4.768	<0.001
	Resident	−0.216	0.238	−0.910	0.363
Year		0.298	0.546		

*Reference category for fixed effects were set to immigrants (= intercept). Random effect (year) estimate is variance and SE column is standard deviation. Distributions used were negative binomial for southern fulmars and Poisson for wandering albatrosses. The zero-inflation model estimates the probability of extra zeros such that a negative coefficient for residents indicates a lower chance of having no recruit. The conditional model estimates the abundance such that a positive effect for residents indicates a higher number of recruits. See Supporting Information Fig. S3, S4 and S5 for model fit.

source populations. Thus, given the dispersal pattern observed in the wandering albatross (Inchausti and Weimerskirch, 2002; Charmantier *et al.*, 2011) most immigrants probably came from other islands of the Crozet archipelago. We recorded one immigrant snow petrel from Casey station (1300 km east of Pointe Géologie), but snow petrels and southern fulmars were marked at only a tiny proportion of their populations.

The lower fitness of immigrants relative to residents may result from local adaptation with immigrants maladapted to their new environment, but also to several nongenetic effects. Immigrants might be less competitive individuals that were unable to remain in their original environment due to external conditions (Clobert *et al.*, 2009), the act of dispersal itself might be costly and could have carry-over effects after settlement in the new environment, and success in the new environment might first require familiarity with the local environment and its residents (Bonte *et al.*, 2012). In seabirds, costs associated with dispersal following settlement could thus be opportunity costs (e.g. loss of evolutionary acquired advantages when settling in a new habitat, unfamiliarity with new foraging areas, poor knowledge of high-quality nesting sites) and risk costs (e.g. higher predation risk in a new breeding colony, new interactions with con- or heterospecifics due to conflicts for nest occupation) (Bonte *et al.*, 2012). Although disentangling the relative importance of these proximate causes deserves further investigation and was outside the scope of

this study, our results support theoretical predictions for how selection might favour the philopatric behaviour of seabirds (Coulson, 2016), which has intrigued biologists due to their high mobility, particularly in albatrosses and petrels (Pinaud and Weimerskirch, 2007).

The costs of emigrating to new colonies appear to be less for female than male seabirds. Indeed, relative to residents, fitness losses of immigrant females were relatively lower than those observed in males. Immigrant female snow petrels even had higher number of chicks fledged and breeding success than residents. This smaller disadvantage (or advantage in the case of snow petrels) to immigration in females is in line with what would be expected if the benefits of remaining philopatric were sex dependent and in favour of female-biased dispersal, as generally observed in birds (Greenwood, 1980; Li and Kokko, 2019). The hypothesis of asymmetric limiting resources predicts that sex-biased dispersal may evolve when the familiarity with local environments benefits one sex more than the other in competition with same-sex individuals (Greenwood, 1980; Li and Kokko, 2019). The sex that benefits more from familiarity with local environment in competition with same-sex individuals should remain philopatric, with higher costs of dispersal for the sex that is responsible for territory acquisition, and lower competitive success of dispersers (Perrin and Mazalov, 1999). In seabirds, including the three species studied here, prospecting for nest sites, defense of territories against competitors or predators are overwhelmingly performed by males (Nelson and Baird, 2001). Our results are thus in line with the hypothesis of female-biased dispersal being driven by asymmetric limiting resources and the competitive ability of dispersers *vs.* non-dispersers.

This study provides clear evidence of lower fitness of immigrants in several long-lived species. One important implication of our results is that estimates of realised gene flow can be biased if the poor reproductive performance of immigrants is not accounted for, with potential consequences for estimates of population structure (Bossart and Prowell, 1998). In species such as seabirds structured in dynamic metapopulations, reduced immigrant fitness may contribute to the maintenance of intraspecific diversity in addition to previously known factors (Friesen, 2015). Reduction in gene flow can also help maintain local adaptation and functional diversity (Nunes and Bugoni, 2018). Our definition of immigrants was straightforward for colonial nesting species such as seabirds. However, for territorial species that do not breed in colonies, immigration costs may be more challenging to measure and vary as a function of dispersal distance (Hansson *et al.*, 2004; Bonte *et al.*, 2012). This requires further research on species with different lifestyles and across the slow-fast gradient of life-histories. Furthermore, in males, immigrants were more likely to experience proportionally greater fitness reduction than residents compared to females, supporting the idea that sex-biased dispersal patterns are understandable in light of sex-specific costs and benefits of philopatry in birds (Greenwood, 1980; Li and Kokko, 2019). These findings raise unanswered questions about the nature of behavioural mechanisms associated with lower immigrant fitness, which poses a major challenge both logistically and methodologically.

AUTHORSHIP

CB conceived the ideas and designed the methodology. CB and KD analysed the data. KD collected, cleaned and managed the data. CB wrote the manuscript with input from KD.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate repository (Dryad, Figshare or Hal) and the data DOI will be included at the end of the article (https://hal.archives-ouvertes.fr/hal-02946865).

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